

Solanopteris brunei, a Little-known Fern Epiphyte with Dimorphic Stems¹

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Although the stems of ferns tend to be of only one basic type—the rhizome—there are a number of striking variations known, both in internal structure and in gross morphology. In size alone, rhizomes vary from the massive upright trunks of certain tree ferns down to the almost filiform structures of many filmy ferns. Very few species of ferns have evolved dimorphic stems showing “division of labor.” Some do have differentiation into short shoots and long shoots, i.e., those with short internodes and those with long internodes. Where dimorphism occurs, it is associated functionally, as a rule, either with vegetative propagation or with storage. For example, the Ostrich Fern, *Matteuccia*, has compact, upright, frond-bearing stems and elongate, horizontal stems. The latter enable the plant to form large colonies or clones. Similar, but even narrower and more specialized “stolons” are found in some species of sword ferns, *Nephrolepis*.

Most examples of drastically modified stems, such as the strongly flattened rhizomes of *Myrmecophila* and *Lecanopteris* or the tuber-like bodies of *Nephrolepis*, *Polypodium*, and the plants to be described below, are epiphytic. Furthermore, they seem to be associated with storage and possibly even symbiotic relationships with ants. Indeed, except for those ferns which have obviously solid “tubers,” practically all of these plants have been referred to as “ant-plants” or “myrmecophytes,” whether or not any obligatory relationships with ants have been observed or experimentally demonstrated.

The plant to be described in this article is a little-known epiphyte with dimorphic stems (*Fig. 1*): ordinary polypodioid rhizomes and drastically modified, “potato-like” hollow tubers. Hagemann (1969, fig. 1) has recently illustrated and described the structure of these tubers in some detail, but he did not concern himself with the broader comparisons of the plant in respect to its other peculiarities and taxonomic relationships. In our investigations of *Solanopteris* we have discovered a number of distinctive characters which are described here for the first time.

The occasion for our study was the discovery in February, 1966, of a fine colony of *Solanopteris* in Costa Rica during a class in tropical epiphytes presented by the Organization for Tropical Studies. A large colony was found growing on a fallen bough of a tree in a deep rain-forest. We searched for the species again in July, 1967, but without success. The forest had been cut down and the original colony destroyed. Since our original find, no one seems to have encountered this plant in

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Fig. 1. Living plant of *S. brunei* showing fertile fronds, unmodified rhizomes, and tubers. Costa Rica, 1966. Photo by Job Kuijt.

Costa Rica, despite extensive explorations by many people. Therefore we believe that this fern is probably a great rarity, although we admit that the lack of collections may be due to its habitat.

Until Dr. Hagemann's recent publication on the tuber-like structures of this fern, little was known about it, even its generic disposition. The plant was described by Wercklé as *Polypodium* (?) *brunei* and so published by Christ. All Christ saw, however, were the tubers he received from Wercklé. For some reason, Wercklé sent no leaves or unmodified rhizomes, although he reported that the leaves were simple and belonged to *Polypodium*. Christ's description, consequently, is very vague, but sufficient to place the specimen we found. This identification was confirmed by matching our specimen with a tuber from the type collection.

The purpose of this report is to give a somewhat detailed description of this species and to place it taxonomically. Although it is unquestionably related to *S. bifrons* (Hooker) Copel., the broader taxonomic relationships of these two species are still uncertain, partly because of the scanty knowledge of the detailed characteristics of the Polypodiaceae.

The genus *Solanopteris* is based upon *Polypodium bifrons* Hooker (Copeland, 1951, pp. 75, 128). The type of *P. bifrons* is a specimen collected near Archidona, Ecuador (Jameson 789, K, fragm US), found on a tree along a river. To this genus must be added:

***Solanopteris brunei* (Wercklé in Christ) Wagner, comb. nov.**

Polypodium (?) *brunei* Wercklé in Christ, Bull. Soc. Bot. Genève, II, 1: 221. 1909. Type: Carrillo, Prov. Limón, Costa Rica, Wercklé (P, fragm MICH).

Climbing epiphytic fern occurring in dense masses (*Fig. 1*) more or less intermixed with other epiphytes on branches of trees in rich forests mostly below 1000 m altitude. Leaves arising between conspicuous, hairy, tuber-like modified stems in which ants and other insects are usually found.

Rhizomes (*Fig. 2*) long-creeping, 1.5–2.5 mm in diam, commonly covered with a white, powdery material upon drying. Leaves 1–3, clustered near the tips of short, lateral shoots borne 1–4 cm distant along the creeping rhizomes; roots scattered, solitary, or clustered. Rhizome apices and young parts of the rhizomes covered with promptly deciduous, golden setae 1–3 mm long and more persistent, round, peltate scales 1 mm in diam. Tuberous rhizomes hollow, produced laterally on short shoots, brown to purplish-brown, 1.5–3 cm in diam, containing a central cavity plus several parietal cavities, these lined with roots originating around the ventral opening. Tuber wall 1.5–3 mm thick, invested with deciduous, golden, peltate-based setae 2–5 mm long and persistent, overlapping, brown-centered, round, peltate scales 0.1–0.3 mm in diam. Leaves dimorphic, bright green, drying brown, chartaceous to subcoriaceous, simple with entire or undulate margins, nearly sessile, the petioles very short with laminar wings decurrent to within 0.5–5 mm of the slightly swollen articulation. Fallen fronds leaving a raised, round scar approximately 1 mm across. Major lateral veins usually subopposite, visible on the adaxial blade surface in dried material, the vein pairs 0.3–0.9 mm distant. Ultimate veins finely reticulate with numerous included free veinlets, these usually with 1–4 short branches (*Fig. 3C, D*). Sterile leaves obovate to oblanceolate with usually broadly rounded apex and entire margin, 1.5–11.0 cm long, 1–2 cm wide (*Fig. 3C*). Fertile leaves linear-lanceolate, 7–25 cm long, 0.4–1.5 cm wide, with

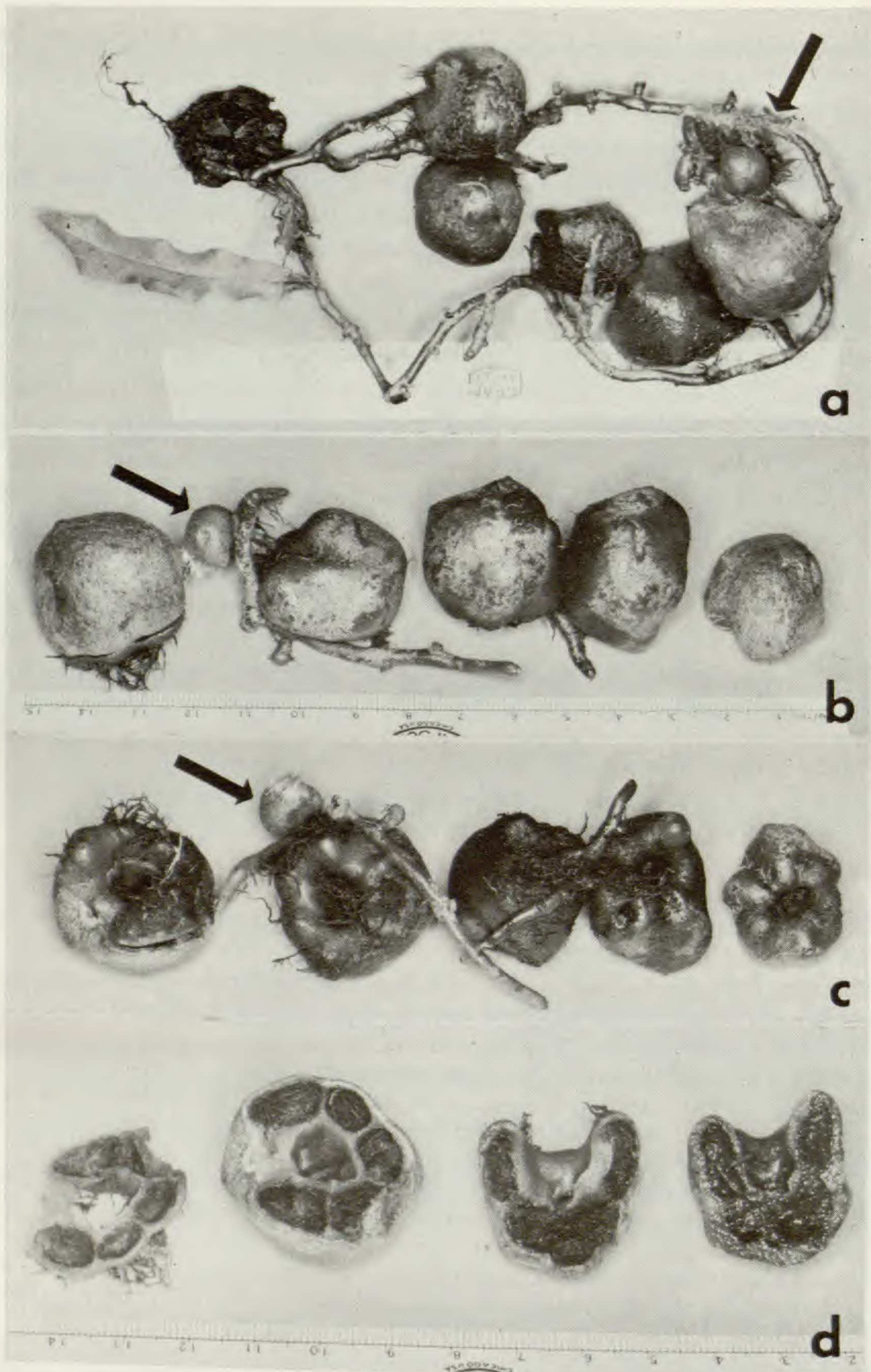


Fig. 2. Stem system of *S. brunei* showing extreme dimorphism. Arrows point to young tubers. Fig. 2A. Stem system with leaf attached. Fig. 2B. Top view of representative tubers. Fig. 2C. Same specimens turned over to show opening. Fig. 2D. Sectioned tubers. At left, sectioned transversely near top to show chambers around central cavity; at right, sectioned longitudinally. Photo by T. L. Mellichamp.

attenuate apex and more or less undulate margins (*Fig. 3D-F*); sinuses, if present, opposite the sori. Sori medial, orange-brown at maturity, subcircular to elliptical, parallel to the midrib, 2–5 mm long, 1–3 mm wide, densely paraphysate, the sporangia obscured, the paraphyses up to 1 mm long, with swollen, flattened, 6(5–9)-celled tips, the medial cells elbow-shaped (*Fig. 5*). Spores spinulose.

Additional specimens examined:

COSTA RICA: Cartago: Pejivalle, *Lankester 810* (US). **Cartago Limón:** About half way between Turrialba and Siquirres, ca 300 m, *Wagner* in 1966 (MICH). **Guanacaste:** El Arenal, 485–600 m. *Standley & Valerio 45173, 45195* (both US). **PANAMÁ: Coclé:** Region N of El Valle de Anton, 1000 m, *Allen 2880, 2899* (both US). **Panamá:** 10 mi S beyond Goofy Lake in Cerro Azul, *Correa & Dressler 176* (MICH, US). **COLOMBIA: Nariño:** 80 km E of Tumaco, Carretera past Tumaco, 150 m, *Hagemann 18926* (MICH).

This fern is evidently more closely related to *S. bifrons* than to any other known species. Hagemann (1969)² concluded that the tubers of *S. bifrons* and *S. brunei* have the same basic structure (with some conspicuous differences) and that they are modified lateral branches of the rhizome. The tuber surfaces usually bear eight low protuberances (*Fig. 2C*), four dorsally, which are homologous to leaf bases, and four ventrally, which correspond to lateral shoots. (Occasionally a single, more or less abortive leaf may be present on the dorsal side of the tuber.) The pith inside the vascular cylinder is destroyed early in development, and the central cavity (*Fig. 2D*) then appears as an opening on the ventral side of the tuber. A network of roots originates around the ventral opening and grows into the cavities, appressed to their walls.

Our present geographical knowledge of *Solanopteris* is very limited. The paucity of collections, particularly of *S. brunei*, must mean that these ferns either are very rare and sporadic, or that they occur normally so high in the forest canopy that they are rarely observed or collected. *Solanopteris bifrons* is known from Colombia to Peru. *Solanopteris brunei* is best known from Costa Rica and Panamá; Hagemann's recent discovery of it in Colombia is the first record for South America.

These two species of *Solanopteris* can be distinguished by the following key:

- Sterile blades entire or slightly undulate, chartaceous to subcoriaceous, rounded at the apex; venation complex, the areoles 1–3 mm long; fertile blades broad, the sori extending up to 1 mm of the margin, the marginal sinuses, if any, opposite the sori; soral paraphyses with 6(5–9)-celled tips, strongly flattened at the apex; tubers with peltate scales and brown at maturity (Costa Rica to Colombia).*S. brunei*
- Sterile blades grossly toothed, the teeth 4–7 mm long, ca 5 mm distant, herbaceous, acute at the apex; venation complex, the areoles 4–8 mm long; fertile blades narrow, the sori extending to the margin, the marginal sinuses between the sori; soral paraphyses with 2–5-celled tips, slightly flattened at the apex; tubers becoming glabrous and white at maturity (Colombia to Peru).*S. bifrons*

² Dr. Hagemann is currently studying yet another species of *Solanopteris* from Peru which has coenosori and the fronds borne on the tubers themselves. Whether or not his material is conspecific with *Polypodium tuberosum* Maxon (*Amer. Fern J.* **33**: 135, 1943), from near La Chonta, Ecuador, remains to be seen.

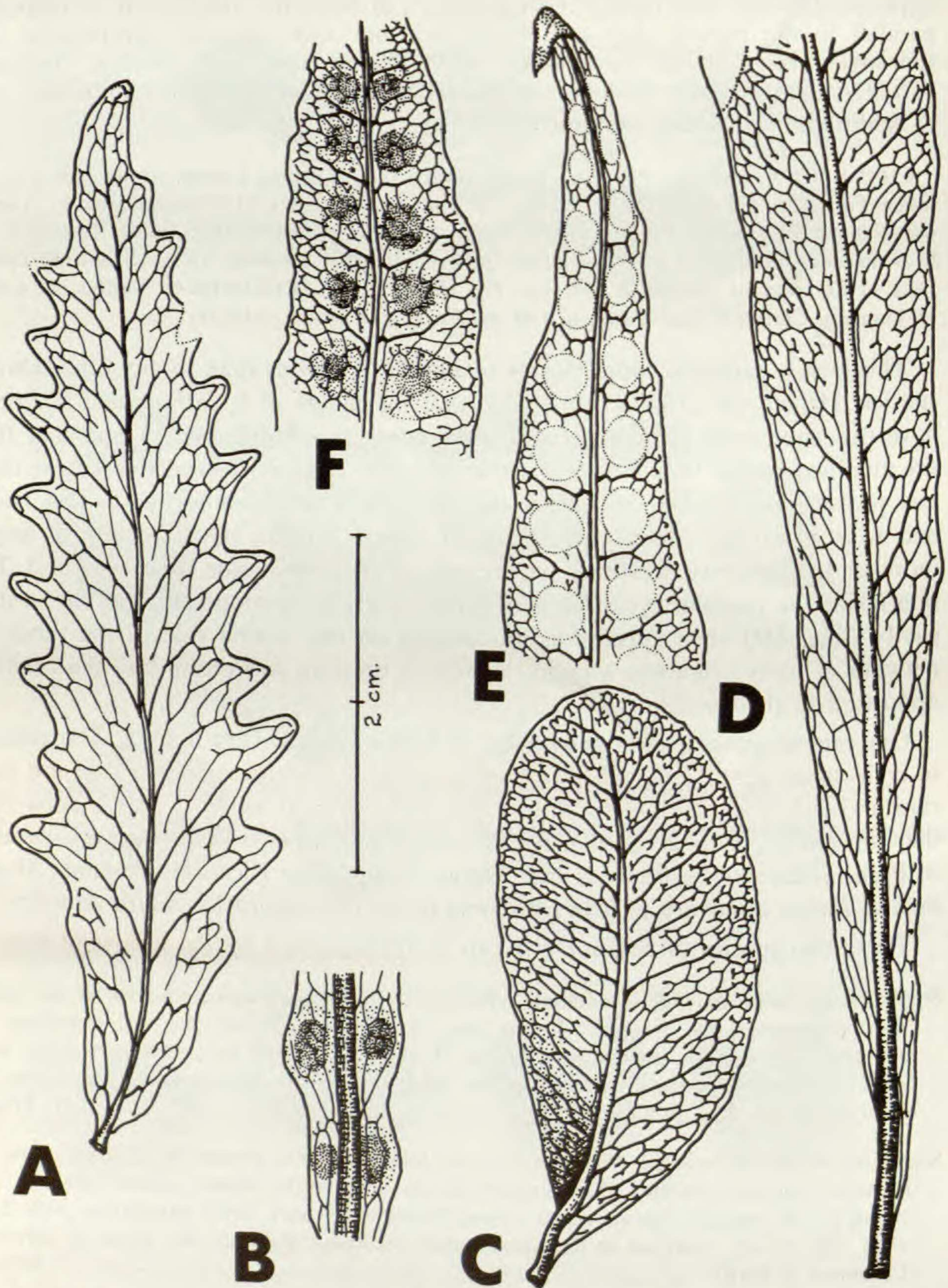


Fig. 3. Venation patterns of *Solanopteris*. Fig. 3A. *S. bifrons*, sterile leaf; Colombia, Klug 1838 (MICH). Fig. 3B. Same, portion of fertile leaf. Fig. 3C. *S. brunei*, sterile leaf, Panamá, Allen 2880 (US). Fig. 3D. *S. brunei*, base of fertile leaf, Costa Rica, Wagner (MICH). Fig. 3E. Same, tip of fertile leaf. Fig. 3F. Same, portion of leaf with sori removed to show fertile veins; the dark stippling represents receptacular area.

GENERIC RELATIONSHIPS

Our knowledge of generic relationships among the Polypodiaceae is still imperfect, especially with respect to *Microgramma* and *Pleopeltis*, which are the genera most closely related to *Solanopteris*. Copeland (1951), in writing of *S. bifrons* alone, stated that *Solanopteris* has

more resemblance to *Microgramma* than to anything else, and this may be its affinity, but the rather fleshy, herbaceous texture, and the laxly and irregularly anastomosing veins, and the paucity of included veinlets make it seem unreasonable to include it in that genus. The tubers are remarkable; but I would not regard them as by themselves justifying generic distinction for the species, no more than do those of *Nephrolepis cordifolia*.

Standing alone, *S. bifrons* might be in question as constituting a genus. However, the presence of at least one strongly divergent additional species, but one which shares its salient characteristics, fortifies the conclusion that *Solanopteris* warrants recognition as a separate genus. In spite of Copeland's comments, the tubers are also strong justification for generic separation. Hagemann's studies reveal that they are remarkably complex, highly specialized structures.

Another character supporting generic separation is the complex, reticulate venation pattern with numerous, irregularly oriented, free included veinlets—anaxetoid venation, as illustrated by Dickason (1946, fig. 20). A few venation patterns are shown for comparison in Fig. 4. The veins of *Campyloneurum*, *Pesopteris*, *Phlebodium*, and *Polypodium* (Fig. 4A, B, E, G) are easily separated from those of *Solanopteris*. But the patterns of the two species of *Microgramma* and of *Microsorium* (Fig. 4C, D, F) are in some ways rather similar to those of *Solanopteris*, the *Microsorium* being somewhat intermediate between the other two genera. Evaluation of venation as a generic character is difficult, for within obviously related groups the variation of patterns may be extreme, as illustrated by Tindale (1960) and de la Sota (1960, 1966).

The other characters supporting separation are the peculiar soral paraphyses, which form a dense mat of uniseriate hairs with dilated apices (Fig. 5), the receptacular area that is served by a complex system of veins (Fig. 2B, F), and the spores, which are covered with narrow spinules.

That these two species, in spite of their common properties, have become so thoroughly differentiated from one another, suggests that they belong to a common lineage, the ancestor of which separated long ago from other polypodioids. *Solanopteris* is surely distinct from *Microgramma* and *Pleopeltis*, both of which lack the tubers, the specialized soral paraphyses, and the spiny spores of *Solanopteris*. In addition, *Microgramma* has simpler receptacular venation.

ECOLOGICAL RELATIONSHIPS

The most intriguing biological question concerning *Solanopteris* has to do with the function of its tubers. It seems difficult indeed to imagine that such specialized structures do not have some definite functional role. One may suggest that these organs are functionally related to storage tubers like those of certain sword ferns or of occasional populations of polypodies (e.g., *Polypodium polypodioides* and

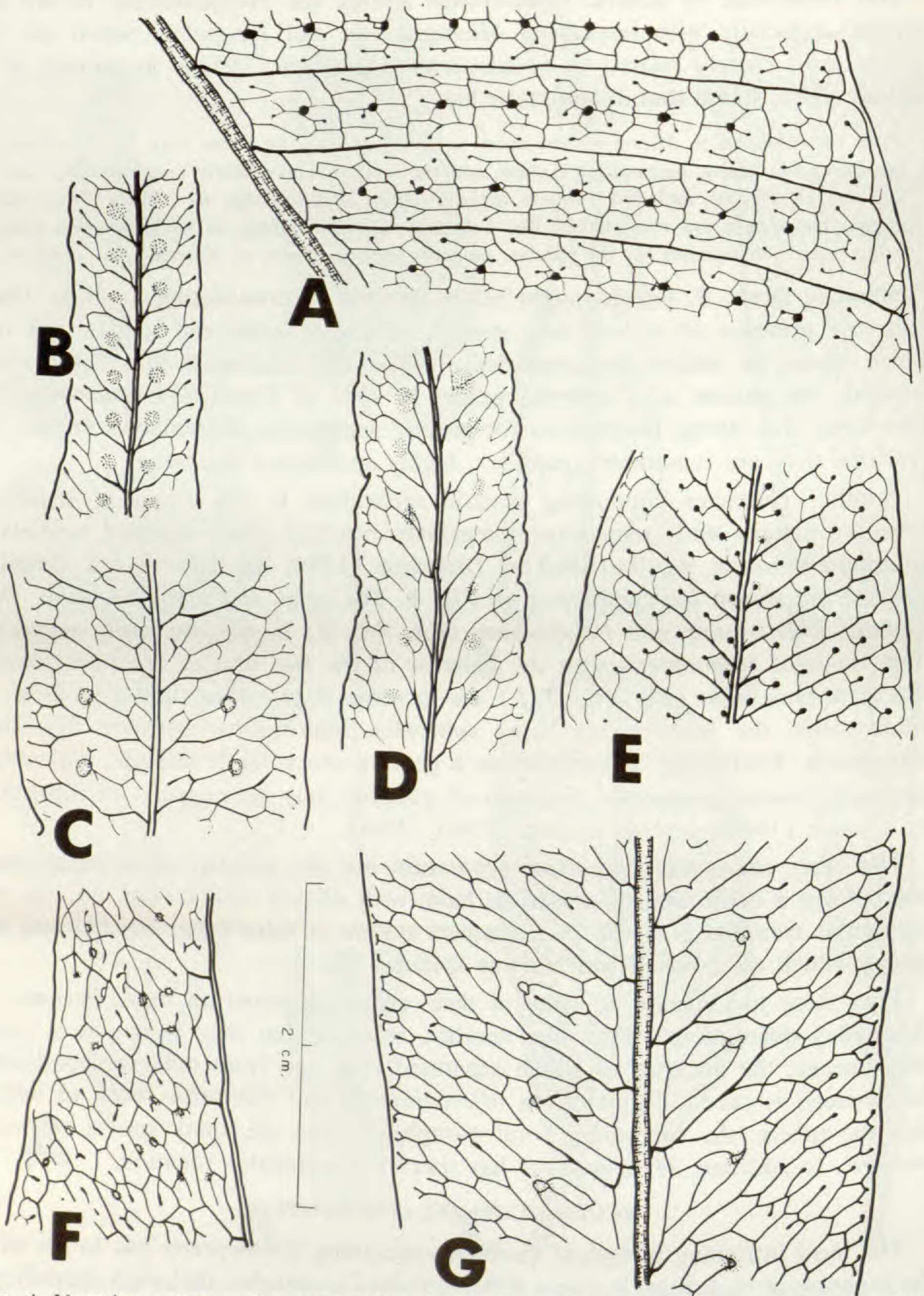


Fig. 4. Venation patterns of several polypodioid genera. Fig. 4A. *Pessopteris crassifolia*. Fig. 4B. *Polypodium* sp. Fig. 4C. *Microgramma lycopodioides*. Fig. 4D. *Microgramma heterophylla*. Fig. 4E. *Campyloneurum phyllitidis*. Fig. 4F. *Microsorium punctatum*. Fig. 4G. *Phlebodium aureum*.

Pleopeltis percussa in Costa Rica). But what physiological adaptation is involved that could bring about selection for the remarkably distinct tubers of *Solanopteris*?

Parallelisms or convergences in rhizome modification are known in certain Old World polypodies which are usually regarded as ant plants (myrmecophytes). They are presumed to be specialized for symbiotic associations with the ants that regularly inhabit their stems, and are divided into two types. The "Myrmecophila" type (e.g., *M. sinuosa* (Wall. ex Hook.) Christ ex Nakai and its relatives) is chiefly Malesian—Polynesian, and has a scaly, somewhat swollen rhizome containing chambers; the "Lecanopteris" type (e.g., *L. carnososa* (Reinw.) Blume) ranges from Sumatra and the Moluccas to the Philippines, and has a naked, extremely flattened, crustose rhizome which looks like a huge fungus sclerotium. Both types have received much attention and speculation from botanical writers because of their ant-filled rhizomes. I do not believe that *Solanopteris* is related to either of these genera, or that the two genera are necessarily related to one another.

Christ (1910, p. 289) based his statements on tuber function in *Solanopteris* on the work of Senn (1910) and Ule (1906). He believed the tubers of *S. brunei* were stems modified to hold water, whereas those of *S. bifrons* were leaves transformed for the same purpose. However, he was so impressed by their resemblances that he also suggested that they might ultimately be shown to be the same (Christ, 1910, p. 98), and Hagemann (1969) concluded that this is true. Bower (1923, pp. 43–44) compared the function of the tubers of both species of *Solanopteris* with that of the similarly specialized leaves of *Dischidia* (Asclepiadaceae), which also have cavities penetrated by roots. Bower's illustration, which is taken from Ule, does suggest *Dischidia*, but is in some ways misleading. Plants of *Dischidia* with which I am familiar show definitely pendent sacs (modified leaves), and there is clearly a more or less exposed opening at the upper end through which the roots enter. In my specimens of *Solanopteris*, the hollow bodies were apparently appressed to the substrate, opened downward, and are hardly what one would expect if the organs were truly water catchers. In Fig. 2, one of the tubers has been twisted upward to reveal the opening. Unfortunately, we do not know what the actual orientation of the plants is. If, for example, the clump of plants faces outward or downward, then the tuber orifices would be in position to collect water.

At the time I collected *S. brunei* I had the definite impression that there was a strong ant relationship. Indeed, I became uncomfortably covered with these crawling insects when I attempted to lift off pieces of the plant from the mass of epiphytes in which it was growing. In a letter to W. R. Maxon, dated December 10, 1949, Paul Allen wrote that:

on the under side of these [spherical bodies] are openings into the hollow interior which [are] invariably inhabited by colonies of a small, but exceedingly bellicose species of ant. These make themselves known on the slightest disturbance of the plant, racing at top speed over your protesting anatomy, until fortune favors them with a particularly succulent spot to clamp on to, which they do with a vengeance.

Allen also wrote in his unpublished manuscript "Orchids of Middle America"

(kindly transcribed for me by Caloway H. Dodson):

A single large tree may support, besides orchids and hepatics, many and extremely diverse kinds of ferns and fern allies, which range from tiny species of *Trichomanes*, scarcely an inch in height, to such unlikely creations as *Polypodium brunei*, whose creeping stems develop clusters of fantastic purple, hairy tubers, harboring in their hollow interiors, militant ants and huge scale insects, the latter turret-like in form.

The reports of ants present in the tubers are not consistent. Although Allen wrote that they were "invariably inhabited" by them, the Standley and Valerio specimens are labelled "often but not always infested by ants." Lankester's specimen annotation was especially interesting: "Gall like excrescences on the rhizomes, massed or single; in section, formed of 4 cells. *No tenants found*. Hairy outside."

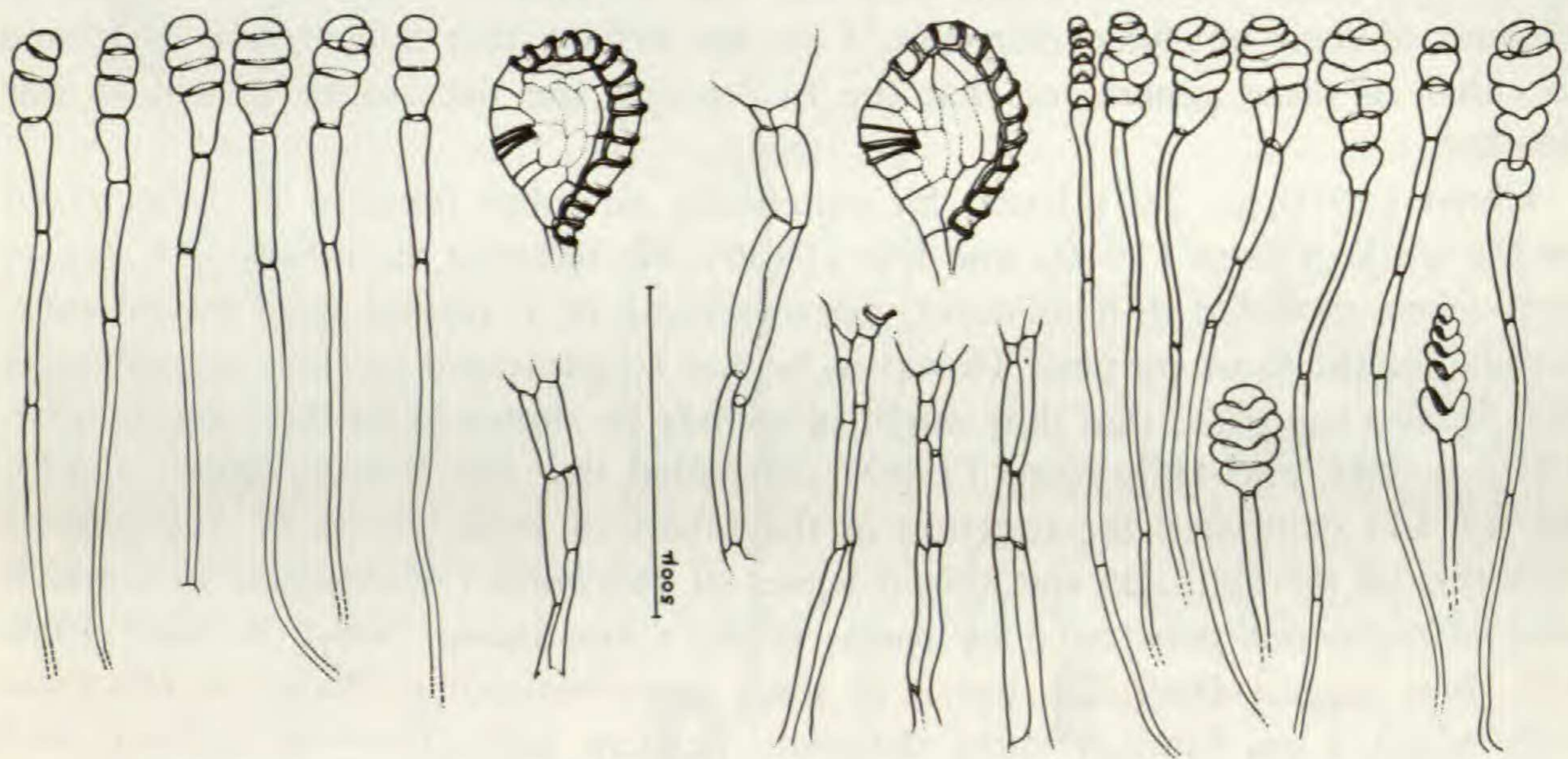


Fig. 5. Soral structures of *Solanopteris*. *S. bifrons*, Colombia, Klug 1838 (MICH) to left of scale; *S. brunei*, Costa Rica, Wagner (MICH) to right.

He apparently later added a postscript reading "*Observed later swarming with ants.*" The collection of Correa and Dressler bears the notes "Fern with rhizome tubers present. Ants living in the tubers." On the contrary, in correspondence with Dr. Hagemann, I received the information that "There were a lot of plants, but I couldn't find any ant within the tubers of the fern." Hagemann also wrote (1969) that myrmecophily in these plants is probably facultative, as Maxon (1943) also implied.

I sent seven tubers of *S. brunei* to Dr. Daniel H. Janzen. He found one worker *Camponotus* sp. in one and three of the same species in another; he found no evidence that this fern is a myrmecophyte. He reported that the ants he found in the *Solanopteris* tubers commonly nest in cavities in rotting wood and, with one or two doubtful exceptions, are not involved with myrmecophytes, except as occasional facultative tenants, anywhere in the world.

The probable function of the tubers of *Solanopteris* remains unclear. More field research is needed, especially on the plants *in situ*.

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RECENT FERN LITERATURE

"SYSTEMATICS OF THE NEOTROPICAL SPECIES OF THELYPTERIS SECTION CYCLOSORUS" (Univ. Calif. Publ. Bot., vol. 59), by Alan R. Smith. vi + 143 pp. 1971. Published by the Univ. of California Press, Berkeley, CA 94720. \$6.50.—Dr. Smith has produced a model monograph, containing morphological, cytological, phytogeographic, ecological, and nomenclatural data, on this taxonomically troublesome group. A detailed and well-illustrated account of gametophyte and sporophyte anatomy and morphology is presented, as is a table of over 60 morphological characters for all the species and varieties; the latter can be used as a multiple-entry key. A considerable number of cytological observations are synthesized into an account of the evolution of the group, and some notes on evolution in the genus as a whole are also given. The dichotomous key, I can report from personal experience, works well, although it is a trifle confusing because of improper indentation between couplets 11 and 12 and 12 and 15. Taxa requiring it are mapped or illustrated with original line drawings or sometimes photographs that are clear and helpful. The nomenclature is carefully reasoned and exceptionally well documented. The discussions accompanying the taxa are especially valuable in contrasting similar species in ways not accomplished by the dichotomous key. Dr. Smith has published his new taxa and combinations under the authority "A. Reid Smith" in order to avoid conflict with another Alan R. Smith, who is also working on pteridophytes in Great Britain. Lists of hybrids, names of uncertain status, excluded names, and representative specimens, and literature cited conclude the volume, which regrettably lacks an index—the only serious defect in an excellent piece of work—*D. B. L.*